COURTSHIP IN PARASITIC WASPS

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Courtship may be defined as any behaviors between conspecific individuals of opposite sex which facilitate mating. Such behaviors, with their incredible variety and obvious importance, have provided biologists with a vast and fascinating field of study. The evolution of such systems has, in particular, received considerable attention in recent years. For the vertebrates, this area has been capably reviewed by Orians (1969) and Trivers (1972).

For the Arthropods, an overview of the evolution of mating systems is provided by Alexander (1964). In addition, studies of courtship behavior have been undertaken in several insect groups, perhaps the most detailed of which are those on *Drosophila* (see Spieth 1974). Yet invertebrate courtship as a whole is still quite imperfectly known, as the parasitic Hymenoptera make abundantly clear.

The parasitic Hymenoptera belong to four superfamilies—the Ichneumonoidea, Chalcidoidea, Proctotrupoidea and Cynipoidea—and include a vast number of small to large insects, the majority of which live at the expense of their phytophagous or carnivorous relatives. In sheer numbers of kinds—i.e., species richness—the parasitic wasps have few rivals. The Ichneumonidae alone constitute one of the largest families of insects, with an estimated 60,000 species placed in 25 subfamilies (Townes 1969), a diversity exceeding that of the well-studied vertebrate class Aves nearly ten-fold. The other major ichneumonoid family, the Braconidae, probably includes close to 25,000 species placed in 18 to 20 subfamilies (Matthews 1974). The classification of Chalcidoidea is not fully agreed upon, but approximately 25 families are recognized, with perhaps as many as 250,000 species in the world. The smallest
superfamily, the Cynipoidea, still includes at least 176 genera and probably over 1400 species (Weld 1952). Best estimates in all groups of parasitic wasps are that only from 10 to 25% of species have even been described. Of course, far fewer have received any serious study.

Parasitic wasps have an almost incredible range of life histories (see Clausen 1940, Doutt 1959, 1964, Askew 1971). The spectrum of hosts attacked is broad, ranging from ticks and spiders to include virtually all orders of insects and all stages of hosts. Yet in one sense they are rather uniform—all adults are free-living, obtaining nourishment from nectar, honeydew, host feeding, etc. Although a few groups (Cynipidae, Agaonidae, Torymidae, Eurytomidae) contain species which exploit phytophagous hosts, no parasitic wasps are known to be predaceous as adults. Thus in courtship, the delicate task of the female needing to discriminate potential mate from potential food (such as in mantids or spiders) does not arise, and the oftentimes elaborate courtship behaviors observed cannot be attributed to this function.

Despite a large number of casual and fragmentary observations, few detailed studies of mating and courtship in parasitic wasps exist. As in other insects, however, parasitic wasp courtship consists of a series of highly specific reciprocal stimulus-response sequences between the sexes. The subfamily Pteromalinae is the best studied to date (van den Assem 1974), and probably the most thorough available analysis of courtship in a parasitic wasp is that of Barass (1960a,b, 1961) on *Nasonia vitripennis*. This small pteromalid, a gregarious external parasite of fly puparia, exhibits almost every component of courtship behavior which has been observed to date in parasitic wasps. Insofar as known, this sequence in the parasitic wasps generally includes most of the following: attraction, recognition, orientation, wing vibration, antennation, head movements, leg tapping, copulation, and post-copulatory grooming.

**PATTERNS IN COURTSHIP: TWO EXAMPLES**

To better appreciate the variety and complexity of parasitic wasp courtship patterns, a close look at two actual cases seems appropriate. Both of the following species have been the subject of some opportunistic preliminary observations in our laboratory during the past year, with 16 mm films through a dissecting microscope allowing subsequent analysis of the courting sequence.

First, let us consider a cynipid, *Diastrophus nebulosus*. This species is widespread in the eastern United States, and produces a distinctive knot gall on wild blackberry, *Rubus* sp. Courtship in *D. nebulosus* is relatively simple, and does not include a wing vibration component. The male first makes antennal contact with